



Sumatran Orangutans and a Yellow-Cheeked Crested Gibbon Know What Is Where

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In their natural habitats orangutans and gibbons have to solve spatial problems to find enough food, which is distributed over large areas and available at different times of the year. Therefore both species should evolve spatial memory skills to remember spatial locations and their content. We conducted 2 studies in a 1900-m² naturalistic outdoor enclosure. In the 1st study, we hid kiwi pieces in 10 different locations and placed kiwi pieces in a visible location. Individuals of both species approached significantly more food locations in the test condition than in the control condition in which no food was hidden. In the 2nd study, we hid 2 types of food in 10 different locations so that individuals had to remember which food type was where. We hid bananas on trees (banana condition) and grapes under bamboo shrubs (grape condition). We also placed oranges in full view (control condition) to rule out the possibility that finding food may automatically trigger an indiscriminate search. Individuals approached the banana locations more often in the banana than in the other 2 conditions. Some orangutans, but not the gibbon, also approached the grape locations more often in the grape than in the other 2 conditions. Individuals often returned to locations in which they previously found food and rarely revisited locations in the same session. We detected little influence of the food quantity and no influence of the distance to each location on the subjects' foraging behavior.

KEY WORDS: foraging; gibbon; orangutan; spatial memory.

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INTRODUCTION

Animals spend considerable time and energy foraging, and individuals that can forage more efficiently have a substantial advantage over others. To forage efficiently, animals have to process different types of information depending on their particular diets. For instance, food-storing scrub jays use and integrate different types of information in their foraging decisions (Clayton *et al.*, 2003a; Clayton and Dickinson, 1999; Emery and Clayton, 2001). They can remember the spatial location of their food caches, the type of items in each location, and the time when they made the caches (Clayton and Dickinson, 1999). Thus, scrub jays can process 3 basic types of information in foraging situations: 1) Where is the food? 2) What kind of food? and 3) When is the food available? The existence of this so-called *www* memory system (Suddendorf and Busby, 2003a) in nonhuman animals and whether it is equivalent to the episodic memory abilities in humans (Tulving, 1983) is a current and hotly debated issue in animal cognition (Clayton *et al.*, 2003b; Suddendorf and Busby, 2003b).

Many primates, with their selective diets scattered over a large area and available for only a limited time, seem prime candidates for the development of a *www* memory system. Milton (1981) argued that the spatial and temporal distribution of scarce but high-quality food resources is one of the basic reasons for the development of intelligence in primates. Previous research on nonhuman primates focused almost exclusively on the Where component. Numerous studies have shown that primates remember the location of food (capuchins: Garber and Paciulli, 1997; Janson, 1998; marmosets and tamarins: Garber and Dolins, 1996; MacDonald *et al.*, 1994; Platt *et al.*, 1996; squirrel monkeys: Roberts *et al.*, 1993; vervet monkeys: Cramer and Gallistel, 1997; yellow-nosed monkeys: MacDonald and Wilkie, 1990; macaques: Menzel, 1991; apes: Menzel, 1973; Gibeault and MacDonald, 2000; MacDonald, 1994; MacDonald and Agnes, 1999). For instance, Garber and Paciulli (1997) conducted a field experiment with capuchin monkeys in Costa Rica. They built a number of foraging platforms within capuchin home range that they baited with bananas or fake bananas, or left empty. Capuchins quickly (after only 1 trial) learned to visit the platforms that contained food and ignored both the empty platforms and the ones baited with nonedible bananas. Garber and Paciulli (1997) also found that the amount of food had a significant influence on foraging decisions. Subjects at first preferentially targeted locations with larger food amounts. In a laboratory study, MacDonald and Wilkie (1990) tested the spatial memory of yellow-nosed monkeys using a win-stay task. They baited 4 of 8 randomly chosen cups and after the subjects had depleted them, they

rebaited them. Within a few trials the subjects showed a preference for cups that had food in the past by inspecting them first.

There have also been several studies with apes. Menzel's (1973) pioneering research investigated the ability of 4 young captive chimpanzees to remember food locations. Menzel hid food in 18 locations in a large enclosure in the presence of 1 chimpanzee. He then returned the chimpanzee to its indoor enclosure, where it waited for ≥ 2 min. After release, subjects that had witnessed the baiting process recovered *ca.* 69% of the rewards whereas subjects that had not witnessed the baiting recovered only *ca.* 6% of the rewards. He also observed that chimpanzees visited locations with larger amounts of food at first. More recently, MacDonald *et al.* investigated the spatial skills of orangutans and gorillas via the same basic methodology that they used for monkeys (MacDonald and Wilkie, 1990; MacDonald *et al.*, 1994). They found that gorillas and orangutans also remembered food locations and foraged efficiently. For instance, they rarely revisited depleted locations on the same sessions but this could have been because the session was terminated after an animal had visited all food sites. Moreover, the orientation of the containers in the gorilla study changed after the subjects manipulated them. Thus, it is possible that gorillas did not revisit empty containers because of their changed appearance.

In contrast to the sizeable literature on the Where component, much less is known about the What component (and as far as we know, no experimental evidence exists to date about the When component). With regard to the What component, Menzel (1991) presented free-ranging Japanese macaques with ripe akebi fruits, a food that grows naturally in the macaques' habitat. However, Menzel presented the fruits out of season so that no other ripe akebi fruits were available at that time in the macaque's habitat. On finding the fruit, subjects looked up in the trees right above where they found the fruit and traveled to other locations where akebi plants can be found. In contrast, when Menzel offered pieces of chocolate (a food that does not naturally occur in the macaques' habitat), macaques consumed them and searched for more on the ground in the immediate vicinity where the original pieces had been found. These findings suggested that macaques knew where vines of particular fruits (akebi) were located in the habitat. In a laboratory experiment, Menzel (1996a,b) presented long-tailed macaques with 2 foods of different quality in their outdoor enclosure. Each type of food was associated with a particular type of landmark in the enclosure. For instance, the high-quality food (i.e., banana) appeared in the vicinity of wooden posts whereas the low-quality food (i.e., carrots) appeared near yellow stones. The macaques' search patterns revealed that they discriminated between the 2 types of food because they searched the locations associated with preferred foods first.

In regard to apes, Emil Menzel's (1973) initial study with chimpanzees also revealed that individuals knew the type of food that was present at each location in their enclosure. He showed juveniles the multiple locations where he hid a highly preferred or a less preferred food. Chimpanzees visited locations with highly preferred foods first. More recently, Charles Menzel (1999) has shown that the female language-trained chimpanzee Panzee can remember the locations of food and its associated content even after a 16-h delay since the baiting took place. She indicated the location and the type of food to naïve humans by means of gestures and lexigrams representing the various items. In a further study, Schwartz *et al.* (2002) investigated the memory of the What and Who components in a gorilla. Different experimenters handed food to the subject and after a retention interval the subject was able to report with the help of a card what he had eaten and who gave him the food.

To summarize, many primate species can remember the locations of food in multiple locations both in the wild and in the laboratory. We know much less about whether they associate certain locations with certain types of food. Most of the experimental data concerns macaques and chimpanzees. The goal of this study was to remedy the scarcity of data on the What component and to produce more data on the Where component for 2 species for which little is known. We tested whether Sumatran orangutans and a yellow-cheeked crested gibbon would remember previously discovered food locations as well as their content. In the wild both species live in an area with a high diversity of plants and a large proportion of their diet consists of fruit available at different times of the year (Delgado and van Schaik, 2000; Leighton, 1987; MacKinnon, 1974). Therefore, according to Milton's theory, both species would be good candidates for the development of advanced spatial foraging skills. They should remember food locations they discovered in the past and also the type of foods at each location. We conducted a laboratory study on a naturalistic outdoor enclosure where we hid different types of food in different locations.

Two aspects of our procedure deserve justification. First, we tested spatial cognition by presenting different types of food in preassigned locations associated with certain environmental features. Thus, bananas appeared in trees of the same species, grapes under bamboo shrubs, and kiwi fruits appeared by fallen logs or tree stumps. The reason for associating features, foods, and locations—as opposed to presenting them independently—was to make the situation as similar as possible to the problems that these species encounter in the wild where a given fruit is always associated with a particular plant or substrate and location. Second, we tested subjects in their social groups rather than individually, for 2 main reasons: 1) Because of the relative small size of the enclosure (1900 m²) subjects may have

incurred negligible costs in moving from one location to another even if they did this inefficiently. The cost-free environment may have obscured the use of efficient foraging strategies. To introduce some cost, and given the impossibility of expanding the enclosure, we increased social competition so that subjects would have an incentive to be efficient in their food search. 2) We were concerned that some subjects may have been extremely reluctant to go outside on their own, and thus we may have failed to obtain any data on them.

EXPERIMENT 1: WHERE IS THE FOOD?

Here we established the basic procedure for the study and tested the hypothesis that orangutans and gibbons were capable of remembering food locations they discovered previously. We selected 10 locations scattered over their outdoor area and baited them with different numbers of kiwi fruit pieces during experimental sessions. We scored how many locations each subject visited after their release in the outdoor area and compared it with control sessions in which we placed no food in those locations.

Subjects

We tested a group of captive orangutans and a single gibbon female (Mini) housed at the Wolfgang Köhler Primate Research Center in the Leipzig Zoo. The orangutan group consisted of 2 adult females, 2 subadult females, 1 infant, and 2 adult males (1 of them unflanged). We introduced an additional adult female orangutan and an adult gibbon male into the group during the study, but the individuals did not take part in the experiment and we kept them indoors while the experiment took place. The infant orangutan also did not participate because the mother always carried it. All of the subjects were born in captivity and had lived in this enclosure for the previous 2 yr. There was an indoor area and an outdoor area. The orangutans and the gibbon females shared the outdoor area, but had separate indoor cages. The subjects were fed 6 times/d. Some feeding sessions took place indoors in the morning and evening and the keeper handed the food to them. Two additional feeding periods took place outdoors in the afternoon in which the keeper distributed the food equally among the subjects by throwing it into the enclosure from an observation tower. While we conducted this study, the orangutans participated in different studies on social and physical cognition but none took place in the outdoor area.

Materials

We conducted the experiment between 0900 and 0930 h in the outdoor area, measuring 1900 m² and enclosed by an electric fence and a 5-m wide water moat (Fig. 1). The orangutans and the gibbon accessed the outdoor area through separate gates. The area was furnished with ropes, trees, a water pond, rocks, natural vegetation, and other elements to simulate the subjects' natural environment and stimulate species-specific behavior. Trees interconnected by ropes facilitated the subjects' use of vertical space. The ground was covered by grass, shrubs, bamboo plants, and other

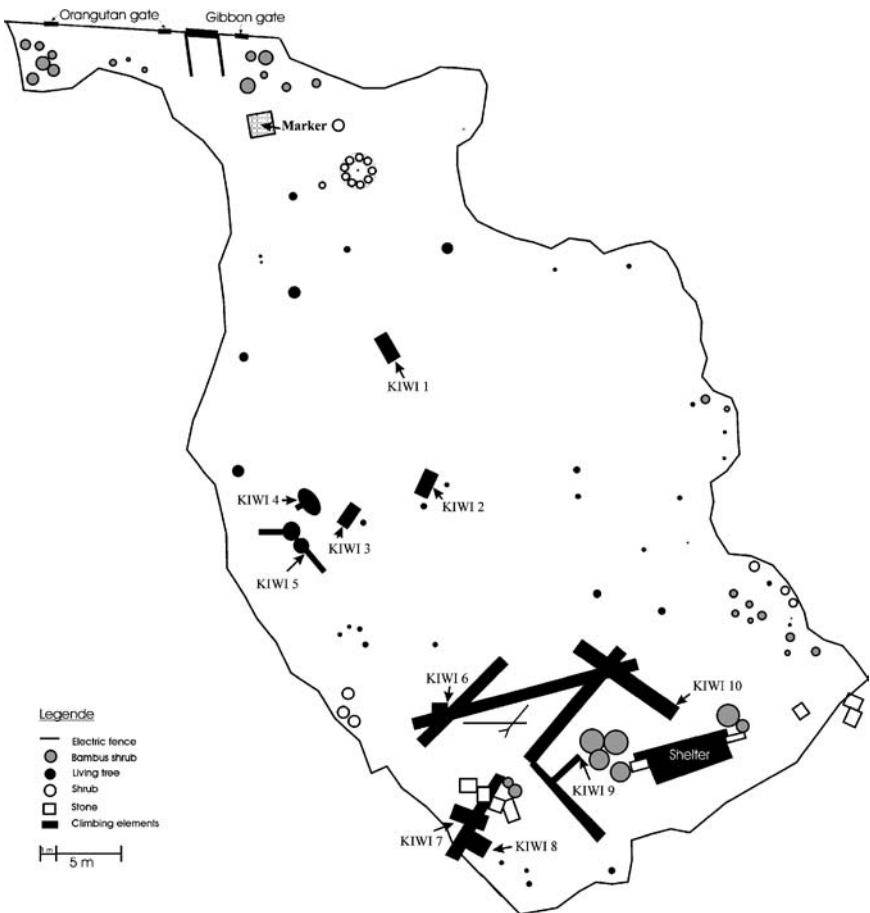


Fig. 1. Orangutan outdoor area (1900 m²) with kiwi fruit locations.

naturally growing vegetation. The area contained also a shelter and a small water pool for drinking. We used pieces of kiwi fruit, a food that all subjects liked. We conducted the observations from 2 observation towers located on opposite sides of the enclosure.

Procedure

Before the study, we observed the movement patterns of the subjects and selected 10 locations that the subjects did not visit frequently (Fig. 1). All locations were on the ground near wooden climbing elements such as logs or trees. We assigned 4–10 kiwi pieces to each, and kept the number constant throughout the study (Table I). During baiting, we kept subjects indoors where they had no visual access to the outdoor area. On experimental days, the experimenter entered the enclosure before the apes had been released and deposited the corresponding amount of kiwi pieces in each location. The experimenter took care to leave no marks, other than the food items, that the animals could use to find the locations. In fact, subjects had to come within 1–2 m to see the food, which was invisible from the enclosure's entry point. She also placed some kiwi pieces by the water pool, which is highly visible to the subjects, to advertise the presence of food to the subjects. On control days, the experimenter placed no food in the outdoor area but also walked to each location to remove the skin of kiwi pieces that the subjects may have left there the previous day. The 2 conditions alternated from day to day. Once the outdoor area was ready and the observers had taken their observation posts, the keeper first opened the gibbon and then the orangutan gates and subjects entered the outdoor area. We conducted the experiment from June 5, 2002 until August 7, 2002 and used a different number of testing days for different subjects because some did not come out during the 30-min observation period (Table II). We dropped 2 testing days for the gibbon because it was outside during hiding.

Scoring and Data Analysis

We observed the subjects for 30 min after their release and scored the following information on a tape recorder: 1) time when an individual visited a location, 2) name of the individual, 3) number of the location the individual visited, and (4) whether it found food and ate it. Our main dependent measures were whether subjects approached the target locations and whether they consumed ≥ 1 items from the target locations. We scored an approach when an individual came within 2 m of a location searching

Table I. Number of food pieces in each location and name of the subjects we observed eating on the corresponding location for the kiwi condition (experiment 1) and the banana and grape conditions (experiment 2)

Location no.	Condition					
	Kiwi		Banana		Grape	
	No.	Subjects	No.	Subjects	No.	Subjects
1	7	T	10 ^{a,b}	T, B, W, Pa, M	4	B
2	10	T, Pi	7 ^b	T, B, W, Pi	5	W
3	5	T, B, Pi, Pa	6 ^b	T, B, W	5	T, B, W
4	6	T, W, Pi	5 ^a	T, W, Pi, Pa, M	8	T, B, Pi
5	6	T, W, Pi	10 ^{a,b}	T, B, W, Pa, M	10	W
6	4	T, W, Pi	5 ^a	T, B, W, Pa, M	5	B, W, Pa
7	8	T, W, Pi, Pa	8 ^{a,b}	T, W, Pa, M	5	B, Pi, Pa
8	5	T, W, Pi, Pa	5 ^a	B, W, Pi, Pa, M	6	B, W
9	5	T, W, Pi, Pa	5 ^a	B, W, Pi, Pa, M	7	B, W, Pa
10	10	T, W, Pi, Pa	4 ^a	B, W, Pa, M	10	B, W, Pi, Pa, M

Note. B, Bimbo; M, Mini; Pa, Padana; Pi, Pini; T, Toba; W, Walter.

^aHidden on rope 5 m high.

^bHidden on biodegradable cord 1.5 m high.

for food, i.e., inspecting and looking at the locations. For most analyses an approach was counted only once per day, except for the revisits analysis—if subjects approached a given location several times in the same day, it would get a score of only 1. Hence the total number of possible approaches per subject was also the number of possible days. We defined consumption as the subject eating ≥ 1 pieces of kiwi at a given location.

Using those dependent variables, we conducted 3 different analyses: 1) a comparison of the approach to the food locations between the

Table II. Age and sex of the subjects and number of days in which subjects participated in each of the conditions in experiments 1 and 2

Name/condition	Age (yr)	Sex	Experiment 1		Experiment 2		
			Kiwi	Control	Banana	Grape	Control
Dunja ^a	29	F	18	17	—	—	—
Toba ^a	8	F	18	17	11	12	12
Bimbo ^a	22	M	12	12	12	12	12
Walter ^a	13	M	16	16	12	12	12
Pini ^a	14	F	17	17	12	12	12
Padana ^a	5	F	17	17	12	12	12
Mini ^b	~ 19	F	18	19	12	10	12

^aOrangutan.

^bgibbon.

experimental and control conditions, including an analysis of the changes that occurred over time; 2) the relationship between approach to a food location and food consumption (amount of success), i.e., whether they preferentially approached locations where they had obtained food in the past; 3) the effect of distance to a location from the starting point and the amount of food it contained on the approach to each location; and 4) whether the individuals revisited an empty location they had emptied themselves in a previous visit.

We used Friedman and Wilcoxon tests to compare the rate of approach to the various locations across conditions both for group and individual analyses. For individual analyses we paired the conditions per session for each subject. For the group analyses we paired the conditions per subject, i.e., mean of individual analyses over all sessions. We predicted that approaches to food locations would be higher in the experimental than in the control condition and thus used 1-tailed significance levels. In addition, we used the Pearson correlation to investigate 1) the relationship between rate of approach and the session (change over time); 2) the amount of success (percentage of approached locations where they ate food items), 3) the amount of food, and 4) the distance for each of the food locations. For the first analysis we paired the number of session with the mean percentage per subject, which means we calculated the mean of approaches across subjects for each session. For the 2nd, 3rd, and 4th analyses we paired the number of approaches at each location with the corresponding values for each location. Because of the exploratory nature of the analyses we opted to use 2-tailed levels of significance.

Results

The mean percentage of locations the orangutans visited across conditions is in Fig. 2. Overall, orangutans visited food locations significantly more often in the kiwi than in the control condition ($T=0$, $p=0.016$, $N=6$), confirmed in the individual analyses in Fig. 3. Four of the 6 orangutans visited the food locations significantly more often in the kiwi than in the control condition (Toba: $T=3$, $p < 0.001$, $N=15$; Walter: $T=0$, $p < 0.001$, $N=14$; Padana: $T=9$, $p=0.004$, $N=13$; Pini: $T=6$, $p=0.003$, $N=12$). The gibbon also approached more often the food locations in the kiwi than in the control condition ($T=0$, $p < 0.001$, $N=13$). Note, however, that the result is based on visiting a single food location (10) during the experiment. In summary, most of the orangutans and the gibbon female approached the food locations more often in the kiwi than in the control condition, suggesting that the discovery of kiwi fruits in one location caused

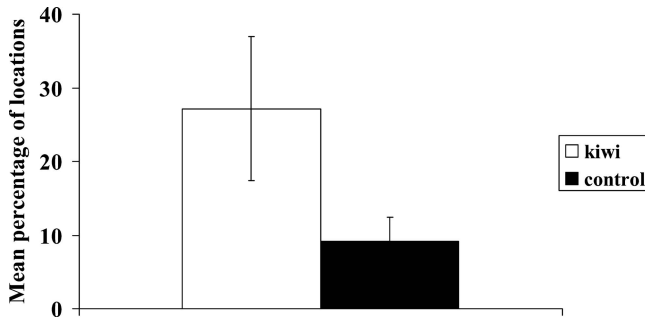


Fig. 2. Mean percentage per subject and standard error of mean of kiwi locations that orangutans approached ($N = 6$) in the kiwi and control condition. Wilcoxon test: $T = 0$, $p = 0.016$, $N = 6$; we scored an approach for a given individual only once per location per session.

them to go to and inspect other locations where they had found kiwi fruits previously.

The mean percentage of locations the orangutans visited over time across conditions is in Fig. 4. In the kiwi condition the percentage of approached locations increased over time ($r = 0.73$, $p = 0.001$, $N = 18$), whereas in controls it remained more or less constant ($r = 0.45$, $N = 17$, $p = 0.07$). Differences between conditions became especially apparent after the 4th day, meaning that initially the animals discovered the food items

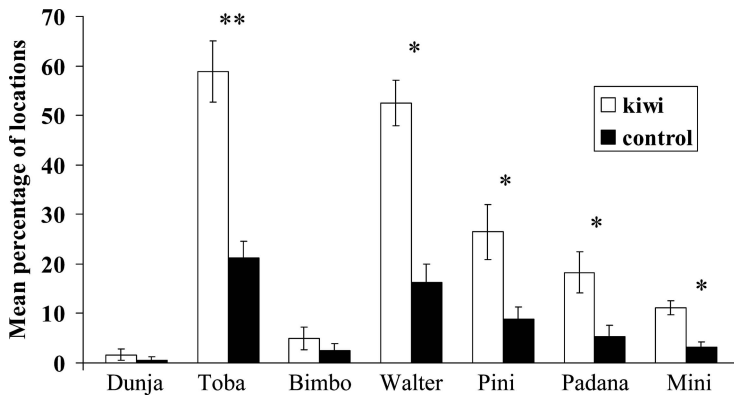


Fig. 3. Mean percentage per session and standard error of kiwi locations that 6 orangutans and the gibbon (Mini) visited in the kiwi and control conditions. Wilcoxon test: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$; we scored an approach for a given individual only once per location per session.

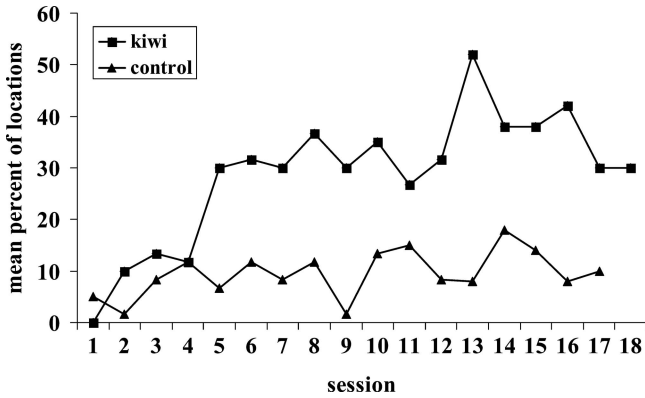


Fig. 4. Mean percentage per subject per session of kiwi locations that orangutans visited ($N=6$) across sessions, comparing the kiwi and control conditions. Pearson correlation: kiwi condition $r=0.73$, $N=18$, $p=0.001$; control condition $r=0.45$, $N=17$, $p=0.07$; we scored an approach for a given individual only once per location per session.

by chance but over time they remembered previously discovered locations and searched directly.

Though by the 4th experimental day the subjects had discovered all kiwi locations, single individuals never visited all locations, but seemed to concentrate on locations they discovered and visited on previous days. For example, the subadult female Toba visited location 2 on all 16 experimental days after discovering the location, but only on 9 of 16 control days. In fact, >1 subject approached an average of 56.6% of visited locations on the same day. Moreover, subjects were very unlikely to approach the same location as others in their 1st visit. Only 12.2% of the initial visits congregated ≥ 2 subjects in the same location.

Thus, we tested whether the number of approaches to a given location correlated with whether subjects had previously found food in that location. The correlation between the percentage of approaches an individual made to a given location and its overall success in obtaining food at that location is in Table III. We defined the percentage of approaches as the number of approaches the individual made to a given location divided by the number of all possible approaches (experimental session) in the respective experimental condition. We defined success as the number of approaches on which the individual obtained food divided by the number of total approaches by the individuals in the kiwi condition. We did not list Dunja in the table because she obtained no food. Three of the 5 orangutans and the gibbon showed a significant positive correlation between approach and success in the kiwi

Table III. Correlation between percentage of approaches and success, amount of food, and distance to the starting point at each location

Name/condition	Success		Food Kiwi	Distance Kiwi
	Kiwi	Control		
Toba	0.71*	0.74*	-0.35	-0.41
Bimbo	0.58	-0.16	-0.27	-0.57
Walter	0.95**	0.66*	-0.18	0.42
Pini	0.59	0.02	-0.10	-0.04
Padana	0.86**	0.69*	-0.11	0.25
Mini	0.99**	1.0**	0.62	0.31

Note. Percentage of approaches is the number of sessions an individual approached a location divided by the total number of sessions; Success correlates the percentage of approach per location with the percentage of success for the kiwi and control conditions. The percentage of success is the number of approaches an individual ate food on a given location divided by the total number of sessions with approach in the kiwi condition. Food correlates the percentage of approaches per location with the number of food items at the corresponding location. Distance correlates the percentage of approaches per location with the distance of the corresponding location to the starting point (water pool). Asterisks denote the significance level: * $p < 0.05$, ** $p < 0.01$.

condition. The other 2 orangutans showed a tendency in the same direction. Moreover, the 3 orangutans and the gibbon that showed a significant relationship between success and approach in the kiwi condition still showed a significant correlation, albeit weaker, between success and approach in the control condition. The subjects thus approached locations in which they had found regularly food in the past.

We also analyzed whether subjects preferentially targeted certain locations based on specific features of the locations. Recall that locations varied both on the distance to the starting point and the amount of food in each location. It is expected that subjects may favor locations with larger amounts of food. We found no correlation between the total number of approaches to a location by an individual and either the distance of the location from the starting point ($r = 0.24$, $p = 0.51$, $N = 10$) or the amount of food in it ($r = -0.27$, $p = 0.46$, $N = 10$; see Fig. 5). The analysis does not take into account, however, whether the individual ever visited the location while it contained food. The individual analyses confirmed the group analysis because we found no significant relationship between approach and distance ($r \leq |0.57|$ for all 6 individuals) or approach and amount of food ($r \leq |0.62|$ for all 6 individuals; Table III).

Finally, we checked whether an individual revisited locations it had already depleted in a previous visit during the same experimental session. Although the food locations were completely depleted in the 1st visit, the fruit skin was left there. Orangutan revisits occurred on average in 5.4%

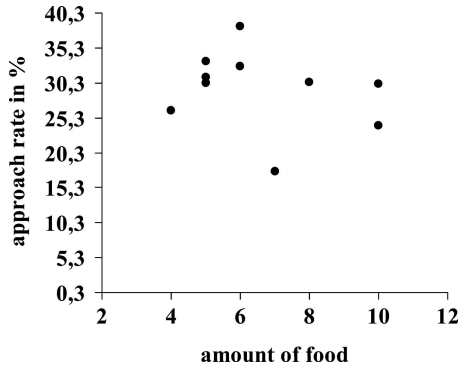


Fig. 5. Mean percentage per subject per location of kiwi locations that orangutans visited ($N=6$) dependent on the amount of food at each location ($N=10$). Pearson correlation: $r = -0.27$, $p = 0.46$, $N = 10$; we scored an approach for a given individual only once per location per session.

($SE = 3.5$) of visits whereas they never occurred for the gibbon. Therefore, subjects revisited food location very rarely.

Discussion

Orangutans and the gibbon visited more food locations in the test than in the control condition and the number of visited locations increased over time, results that were also apparent at the individual level for 4 of the 6 orangutans. Three of the orangutans and the gibbon focused their search on locations where they had discovered food several times in the past. In contrast, there was no effect of food density and distance to the starting point on the subjects' foraging decisions, meaning that the subjects did not preferentially target locations with higher food quantities or that were closer to the entry point. Finally, the subjects avoided revisiting locations they themselves had emptied in previous visits during the same sessions, suggesting they remembered their own actions during the session.

Thus, the results of the first experiment supported the hypothesis that orangutans and gibbons remember the location of previously discovered food. They showed spatial memory skills similar to those of other primates tested under comparable situations (MacDonald and Agnes, 1999). A possible limitation of our study is that subjects may have found more food

in the test than in the control condition because finding food may have put them in a foraging mode. In this way, they would have visited more locations because of an increased level of activity rather than the memory of the food locations. To rule out this possibility, in the next experiment we presented 2 sets of food locations—1 set for each type of food, which also allowed us to investigate whether individuals could not only remember the food locations but also what type of food was where. The skill seems particularly important for frugivorous species that have to keep track of multiple locations and multiple plant species often available only for a short time.

EXPERIMENT 2: WHAT IS WHERE

We selected 20 new locations in the outdoor area, and baited 10 locations with bananas and 10 with grapes on different sessions. Thus, subjects encountered 2 different types of food on different days scattered over 10 locations in the outdoor area. In addition to the banana sessions and grape sessions we included control sessions in which we placed no food in the outdoor area except for oranges in a single visible location. The idea was to see if on finding one type of food at a given location subjects preferentially targeted the other locations associated with that particular type of food in the past.

Subjects

Five orangutans (3 females, 2 males) and 1 gibbon female took part in the study. We excluded Dunja because she did not show any motivation to search for food in the previous experiment but she was still present during the experimental sessions. A new adult orangutan female joined the group on the last 2 sessions of each condition but we excluded her from the study because she found no food in any condition.

Materials

The experiment took place in the same outdoor area as the previous experiment from August 19, 2002 until October 18, 2002. We used bananas, grapes, and oranges as rewards, foods that all subjects liked (Fig. 6).

Procedure

We used the same procedure as in experiment 1 except that we used 2 different types of food (banana vs. grape) in experimental days

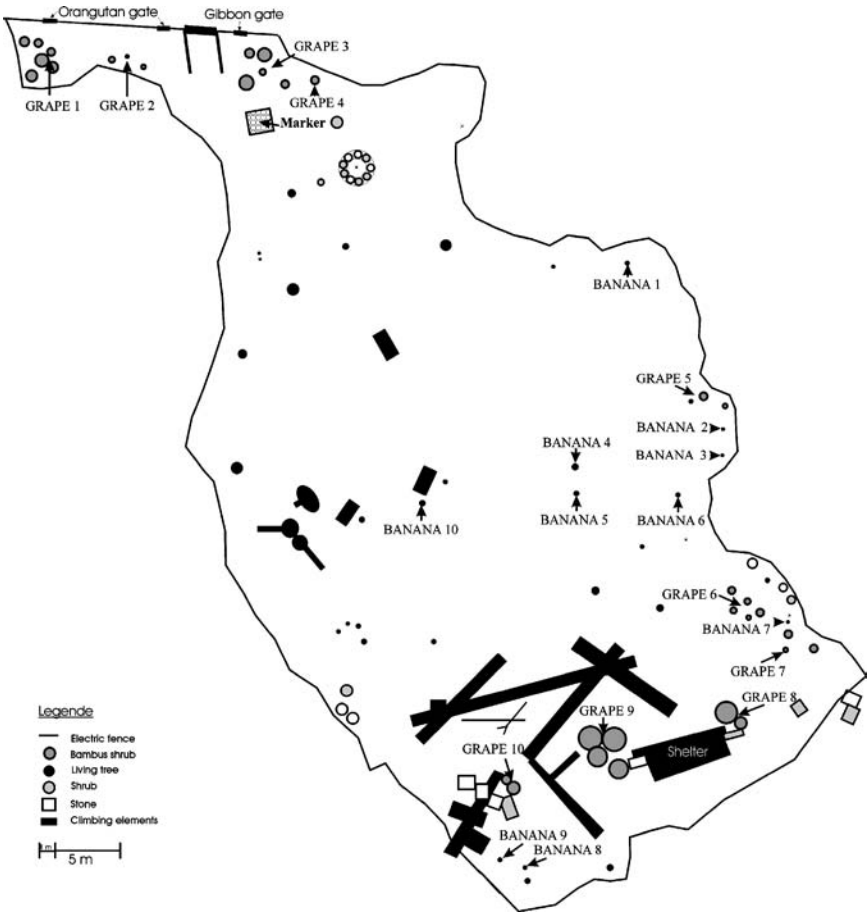


Fig. 6. Orangutan outdoor area (1900 m²) with banana and grape locations.

and oranges in control days. Thus, there were the following 3 conditions:

1. Banana: We selected 10 new locations in the outdoor area and placed 4–10 pieces of banana that we kept constant throughout our study (Table I). All locations were on 10 different trees of the same species (*Acer pseudoplatanus*). The banana pieces were hidden in trees 1.5–5 m high and attached to them with biodegradable cord that remained in place in all conditions but that we baited only in this condition. We positioned the banana pieces at the back of the trees so that they were not visible from the enclosure’s entry point.

We also placed some banana pieces by the water pool so that subjects could see them as they came out.

2. Grape: This condition was analogous to the banana condition except that we selected 10 locations near bamboo shrubs and placed predetermined amounts of grapes at each location. Grapes were not visible from the enclosure's entry point. As before, we also placed some grapes by the water pool.
3. Control: We presented pieces of oranges only by the water pool, so there were no hidden food pieces in the enclosure in this condition. This condition was implemented to rule out the possibility that subjects simply started searching for food once they encountered any kind of food by the water pool.

Once we completed the baiting, we proceeded in the same way as in the previous experiment. We released the subjects and the observers collected the data using the same procedure as in experiment 1. Each individual received 12 d per condition except for Toba, which received 11 d in the banana condition (Table II). For technical reasons grape locations 1 and 5 were not accessible on 6 d of each condition, and we corrected the data accordingly. We also discarded 2 experimental days in the grape condition for the gibbon female because she was outside during the hiding process. We tested the 3 conditions in blocks of 3 d, with each block containing 1 condition per day; i.e., we needed 3 d to complete 1 block. We randomly determined the order of condition in a block. We used the same scoring and analytical methods as in experiment 1.

Results

The mean percentage of banana and grape locations the orangutans visited across conditions is in Fig. 7. Focusing on the banana location, there were differences in the percentage of visits across conditions (Friedman test = 7.6, $df = 2$, $N = 5$, $p = 0.022$). Orangutans visited banana locations more often in the banana than in the grape ($T = 0$, $p = 0.031$, $N = 5$) or control condition ($T = 0$, $p = 0.031$, $N = 5$). In contrast, there is no significant difference between the grape and the control condition ($T = 3$, $p > 0.05$, $N = 5$). Focusing on the grape location, there were also differences in the percentage of visits across conditions (Friedman test = 7.6, $df = 2$, $N = 5$, $p = 0.022$). Orangutans visited grape locations more often in the grape than in the banana ($T = 0$, $p = 0.031$; $N = 5$) or control condition ($T = 0$, $p = 0.031$, $N = 5$). In contrast, there is no significant difference between the banana and the control condition ($T = 5$, $p > 0.05$, $N = 5$).

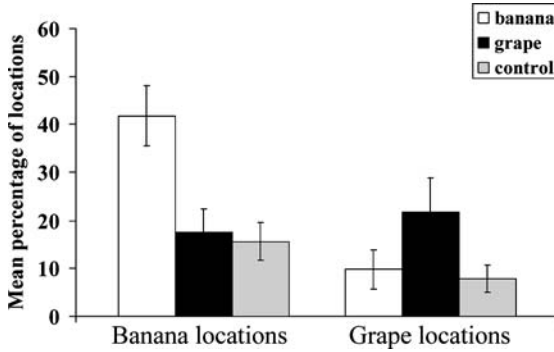


Fig. 7. Mean percentage per subject and standard error of mean of locations that orangutans visited ($N = 5$), comparing banana, grape, and orange conditions. Friedman test: banana locations: $F = 7.6, df = 2, N = 5, p = 0.022$; grape locations: $F = 7.6, df = 2, N = 5, p = 0.022$; we scored an approach for a given individual only once per location per session.

The individual analyses in Fig. 8 confirmed this result. Focusing on the banana locations indicated that 4 of the 5 orangutans showed the same pattern as the overall analysis, thus targeting banana locations significantly more often in the banana condition than in the other conditions (Fig. 8a). Likewise, 3 of the 5 orangutans significantly targeted grape locations in the grape condition compared to other conditions (Fig. 8b). Though Pini in the banana locations and Toba in the grape locations also showed a similar tendency, their results did not reach a significant difference across conditions. Finally, the gibbon also approached more often the banana locations in the banana condition than in the other location. The gibbon also approached the grape locations significantly more often in the grape condition than in to other conditions. Note, however, that the result is based on visiting a single food location (10) during the experiment. In summary, most of the orangutans and the gibbon female selectively approached food locations in which a given type of food was presented, suggesting that individuals were also able to remember what food is where.

The mean percentage of banana and grape locations orangutans visited over time across conditions is in Fig. 9. Focusing on the banana locations (Fig. 9a), a cubic model represented the best fit for the banana condition ($r^2 = 0.69, df = 8; p = 0.0255$) whereas no model produced a satisfactory fit for either the grape or the control conditions. Differences between the banana and the other conditions became apparent from the first day. Regarding the grape locations (Fig. 9b), a linear model represented the best fit for all conditions (grape: $r^2 = 0.67, df = 10; p = 0.0011$; banana: $r^2 = 0.78,$

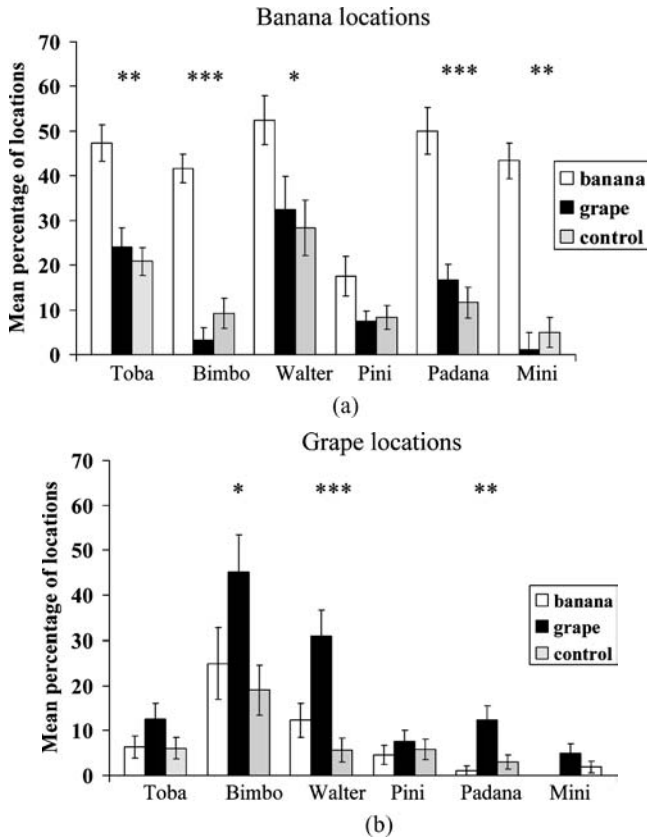


Fig. 8. Mean percentage per subject and standard error of mean of locations that 5 orangutans and the gibbon (Mini) visited, comparing banana, grape, and orange conditions. Friedman test: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. **(a)** Banana locations and **(b)** grape locations; we scored an approach for a given individual only once per location per session.

$df = 10$; $p = 0.0001$; control: $r^2 = 0.77$, $df = 10$; $p = 0.0002$). Differences between the grape and the other conditions became consistent from the 4th day on.

Subjects had discovered all banana and grape locations by the 2nd and last day of testing, respectively. As in the previous experiment, individual subjects never visited all locations, but concentrated on a subset of locations. On average >1 subject approached 61.2% of the visited locations on the same day. Moreover, subjects were very unlikely to

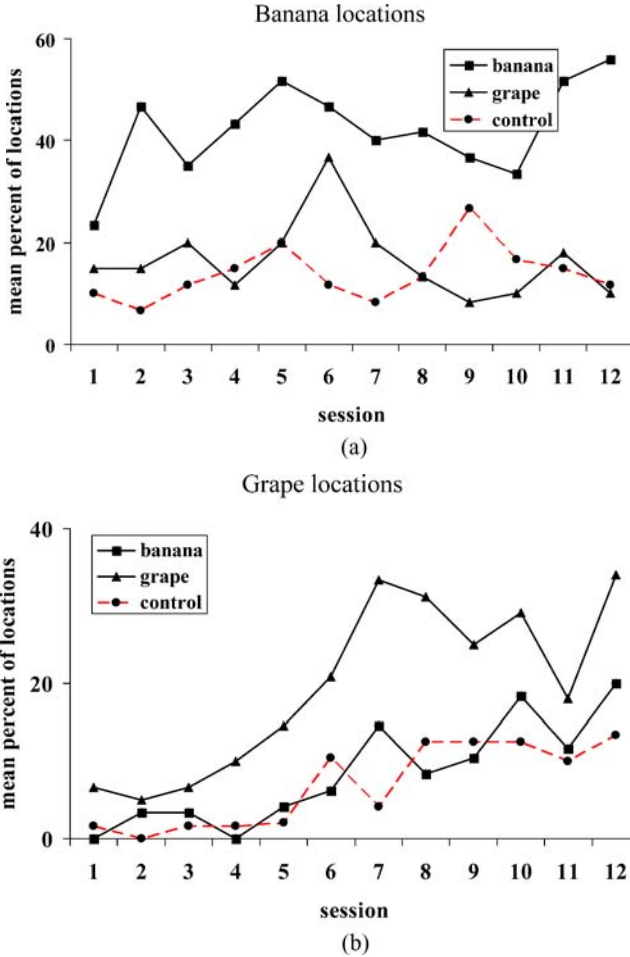


Fig. 9. Mean percentage per subject per session of locations for each session that orangutans visited ($N = 5$), comparing banana, grape, and orange conditions. **(a)** Banana locations; **(b)** grape locations. We scored an approach for a given individual only once per location per session.

approach the same location as others in their first visit. Only 11.2% of the initial visits congregated ≥ 2 subjects in the same location.

We also tested whether the number of approaches to a given location correlates with whether subjects had previously found food in that location. Table IV shows the correlation between the percentage of approaches to the banana or grape locations and the respective success at the locations.

Table IV. Correlation between the percentage of approaches and success, amount of food, and distance to the starting point at each location

Name/condition	Success		Food		Distance	
	Banana	Grape	Banana	Grape	Banana	Grape
Toba	0.99**	0.89**	0.75*	0.34	0.65*	-0.40
Bimbo	0.88**	0.67	0.625	0.37	-0.42	0.82**
Walter	0.54	0.94**	0.75*	0.36	-0.17	0.55
Pini	0.09	0.15	0.159	0.06	0.13	0.60
Padana	0.94**	0.97**	-0.347	-0.13	0.48	0.49
Mini	0.99**	1.00**	0.134	0.57	-0.63	0.281

Note. Percentage of approaches is the number of sessions an individual approached a location divided by the total number of sessions. Success correlates the percentage of approach per location with the percentage of success for the banana and grape condition. The percentage of success is the number of approaches an animal ate food on a given location divided by the total number of sessions with approach in the banana and grape condition. Food correlates the percentage of approaches per location with the number of food items at the corresponding location. Distance correlates the percentage of approaches per location with the distance of the corresponding location to the starting point (water pool). Asterisks denote the significance level: * $p < 0.05$, ** $p < 0.01$.

Three of the 5 orangutans and the gibbon showed a significant positive relationship between approach and success in the banana locations while 1 additional orangutan showed a tendency in the same direction. Subjects showed a similar pattern in the grape locations. Three of the 5 orangutans and the gibbon showed a significant relationship between approach and success, supporting the idea that subjects approached locations that had yielded food in the past.

We also analyzed whether subjects took into account certain features of the problem such as the distance to the food locations or the amount of food at each location. We analyzed the banana and the grape locations separately. There was a significant correlation between the amount of food at each banana location and the approach rate ($r = 0.89$, $p < 0.001$, $N = 10$, Fig. 10a) but no significant relationship between the approach and the distance to the starting point ($r = -0.360$, $p = 0.307$, $N = 10$). Individual analyses confirmed the positive relationship between approach and amount of food for 2 orangutans and also found a significant relationship between approach and distance to the starting point for 1 other orangutan. In regard to grape locations, there was no relationship between the approach rate and the food quantity ($r = 0.39$, $p = 0.27$, $N = 10$; Fig. 10b). In contrast, there is a significant negative relationship between the approach rate and the distance from the starting point to each location ($r = -0.65$, $p = 0.042$, $N = 10$). Yet, individual analyses revealed a significant negative correlation between approach and distance to the starting point for just 1 orangutan.

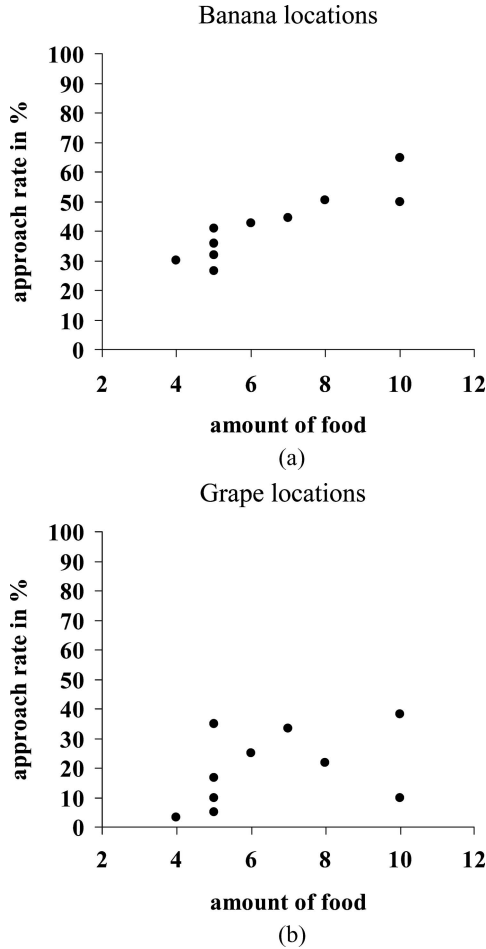


Fig. 10. Mean percentage per subject per location of locations that orangutans visited ($N=5$) dependent on the amount of food at each location ($N=10$). Pearson correlation: (a) banana locations: $r=0.89$, $p < 0.001$, $N=10$; (b) grape locations: $r=0.39$, $p=0.27$, $N=10$. We scored an approach for a given individual only once per location per session.

Finally, we checked whether the subjects revisited locations. The orangutans as well as the gibbon showed a higher revisit rate for the banana locations (orangutans: mean = 18.7%, SE = 2.4; gibbon: mean = 16.7%, SE = 5.3) in comparison to the grape locations (orangutans: mean = 6.2%,

SE = 2.8; gibbon: mean = 0%, SE = 0). Therefore, overall revisits for both locations remained low.

Discussion

Subjects approached significantly more banana locations in the banana condition than in the grape condition whereas they approached significantly more grape locations in the grape condition than in the banana condition. Moreover, subjects did not differentially approach the banana or grape locations in the control sessions when oranges were available, meaning that one cannot explain the increase in visits detected in the test condition of experiment 1 solely by the presence of food at the pool. The general foraging mode hypothesis is unlikely for 2 reasons: 1) Subjects in the control condition of the current experiment found oranges on entering the enclosure but this did not lead them to increase their inspections of other locations as much as finding banana or grapes did. 2) On finding one of the 2 target foods (e.g., bananas), they preferentially targeted locations with the same type of food, not the alternative (i.e., grapes). If a general foraging mode was operating, we would expect subjects to search in all locations that they knew had contained food in the past—but this was not the case. Subjects preferred to visit locations where they found food in the past that corresponded to the food they found during the current session.

Overall subjects performed better at the banana than at the grape locations. One possibility is that subjects preferred bananas over grapes. However, this is not the case; in fact, the opposite is true: subjects preferred grapes over bananas. Another reason is that subjects may have detected the banana locations (trees) more easily than the grape locations (ground), an idea is supported by the fact that subjects discovered banana locations earlier than grape locations, even though neither were visible when subjects entered the enclosure. Indeed, subjects had to get within 1–2 m to see the actual food items. The gibbon's performance was particularly interesting. She discovered several banana locations but only 1 grape location and in the previous study, only 1 kiwi location. We suggest that the gibbon's preference for tree rather than ground locations may be the result of higher detection rate in trees and better escape possibilities.

Unlike the previous experiment, the analysis of location features provided some positive results depending on the type of food. In particular, there is a significant relationship between approach and food quantity on the group level as well as for 2 single orangutans in banana sessions. That is, subjects preferentially targeted banana locations with larger food quantities. In contrast, there is no such effect for grape locations. Perhaps the

different disposition of the bananas and grapes could explain these differences. The fact that some banana locations were distributed at 2 different heights (1, 5, and 7: Table I) may have created the possibility of 2 subjects eating at the same location, thus increasing the chances that the locations would receive more visits.

There is a correlation between approach and distance to the starting point for grape locations but only for 1 subject (Bimbo, Table IV). He approached more often locations that were farthest from the starting point. There is no such effect for the banana locations. All together the correlation between approach and food quantity as well as for the distance to the starting point seemed quite inconsistent. Therefore we suggest that the components seem to be less important for foraging decisions.

Subjects revisited banana much more often than grape locations, which was surprising because they removed the biodegradable cord of some banana locations, thus leaving a cue of their previous visit. Indeed, MacDonald (1994) found that gorillas appeared to use the orientation of depleted containers to avoid revisiting emptied containers. Again, the reason may be that we placed the food in some banana locations (1, 5, and 7: Table I) at 2 different heights: 1) food pieces attached by a biodegradable cord in 1.5 m height and (2) food pieces hidden on a rope 5 m in height. It is conceivable that when the apes visited the banana locations for the first time, they consumed the banana flesh and discarded the peel, which fell to the ground. Later, subjects returned and searched the grass at the bottom of the locations to eat the banana peels or banana flesh pieces that may have fallen during their initial visits.

In summary, the results of experiment 2 supported the findings of experiment 1 in which subjects remembered the location of food sources. Further, we found that the orangutans and the gibbon remembered not only a food location but also its contents. Finally, the results ruled out the possible explanation that subjects visited more locations in test sessions because they had encountered food in the same sessions and that put them in a foraging mode.

GENERAL DISCUSSION

Orangutans and gibbons remembered the spatial position of food locations. The results of orangutans and the gibbon are comparable to those of many other primate species (Garber and Dolins, 1996; Garber and Paciulli, 1997; Gibeault and MacDonald, 2000; Janson, 1998; MacDonald, 1994; MacDonald and Agnes, 1999; Menzel, 1973; Platt *et al.*, 1996). Further, subjects associated certain spatial locations with certain food items,

meaning that they showed the ability to process ≥ 2 components of the foraging cognitive suite: what is where.

Though in general one can say the subjects showed good memory for locations, the precise nature of the information encoded remains unclear. One possibility is that they remembered the precise geographical coordinates for each food location without taking into account landmark information. For example, to visit banana location 1 subjects may have encoded that one has to move straight in a given direction and turn to the right after walking for a certain amount of time. Alternatively, they may have taken into account the presence of particular landmarks that we purposefully associated with the presence of certain types of food. Thus, bananas appeared in trees, grape under shrubs, and kiwi fruits by fallen logs or tree stumps, making the situation as similar as possible to the problems that they encounter in the wild—where a given fruit is always associated with a particular plant. The importance of landmarks in foraging behavior has been established in primates and nonprimate animals (Cheng and Spetch, 1998; Deipolyi *et al.*, 2001; Garber and Paciulli, 1997; Menzel, 1996a,b). In fact, several studies with nonprimates have shown that different species are capable of using different types of information such as landmarks, geometrical cues, or external information sources such as the sun position or the magnetic field to forage and navigate in space (Cheng and Spetch, 1998). Our current data do not allow us to assess the relative contribution of geographical vs. landmark information. Future studies in primates can proceed in 2 directions to resolve the lack of knowledge. One involves the administration of tests in featureless landscapes such as a sandbox with buried food (Hemmi and Menzel, 1995). Another consists of placing new food sources by landmarks that have been associated with food in other locations (Menzel, 1996a,b) and seeing if subjects could transfer the information to completely new locations associated with the same landmark.

An interesting and somehow unexpected outcome of our study was that subjects performed better when the food appeared on trees than on the ground. Recall that they learned the locations of bananas, which always appeared in trees, faster than those of kiwi fruits and grapes, which always appeared on the ground. Because the subjects could not see any of the food items from the enclosure's entry point, we can rule out an initial differential visibility of the food items as a possible explanation for these results. Likewise, the presence of the cords used to fasten the banana pieces to the trees cannot explain this result either because the cords were present in all conditions. Provided that there is not a simple explanation for the result, such as the food on trees has a higher visibility than that on the ground, the results may indicate that foraging off the ground represents a special

adaptation for arboreal species such as orangutans and gibbons. Consequently, testing 3-dimensional spatial knowledge would be essential to find out the full potential of the species.

In general, subjects visited locations in which they had previously obtained rewards and rarely revisited locations in the same session. A possible exception was in the banana condition in which subjects revisited locations to gather previously discarded banana peels. Even in such cases, subjects showed a revisit rate <19%, suggesting that individuals took their own actions into account and avoided approaching previously visited locations. Data of different primate species confirm this result (Cramer and Gallistel, 1997; Janson, 1998; MacDonald, 1994; Menzel, 1973).

Despite efficient deployment of their visits, subjects were not totally exhaustive in their searches within a session because they failed to visit all locations they discovered in previous days. A possible explanation for this result may be the presence of conspecifics during the test. MacDonald and Agnes (1999; *cf.* Gibeault and MacDonald, 2000) found that a subordinate orangutan visited all possible locations if they tested it alone. As soon as they tested it together with a dominant orangutan it stopped visiting all locations. The authors suggested that the behavior could be an effect of competition because the individual avoided visiting a location that a group member had previously visited. We also found that subjects overlapped very little in the locations they chose for their first visit, meaning that they did not simply follow another individual but remembered the location by themselves. When we considered all visited locations within a session, subjects shared *ca.* 60% of their locations with others and often at different times during the session. The higher percentage of overlap in relation to all discovered locations is not remarkable considering that the subjects remembered more than the half of locations over time and of course the probability of overlaps increased. Though we could have tested the individuals separately, we opted not to because a lack of competition may have erased any effects on efficiency. To introduce some cost in the foraging task we balanced the lack of large distances in our enclosure with increased social competition. In the absence of the latter, subjects may have simply visited all locations in no particular efficient order or strategy. Second, we were concerned that some subjects may have been extremely reluctant to go outside on their own, and thus we may have failed to obtain any data on them.

In contrast to other primate studies we found no clear effect of the amount of food in the individuals' foraging decisions. Menzel (1973) and Cramer and Gallistel (1997) showed that chimpanzees and vervets, respectively, preferred to go to the location with the larger amount of food. Similarly, capuchins visited first locations with a larger compared to a smaller amount of food (Garber and Paciulli, 1997). MacDonald and Agnes (1999) found mixed results for orangutans because only 1 of 2 subjects visited first

the location with the larger amount of food. We found mixed results depending on the food locations: a positive relationship between the number of visits and the amount of food for banana locations but not for kiwi and grape locations, but we could not confirm even the positive relationship at the individual level. Because these same apes can satisfactorily solve relative numerosness problems involving discrimination of quantities (Hanus *et al.*, 2003: discrimination ratio ranged from 1 to 5 grapes), it seems that the negative results are due to other factors besides insensitivity to food quantities. One possibility is that individuals did not have a chance to discover the quantitative features of the locations because they visited few locations, or locations with only small differences. However, we can rule out this possibility because the majority of individuals visited more than half of the locations (Table I) in each condition and still did not show a significant relation at the individual level. For example, the orangutan female Toba visited all kiwi locations with 4–10 food items and obtained the food but did not visit locations more often that contained a higher amount of food items. It seems more likely that social competition may have masked the effect of food quantity on foraging decisions.

Taken together, our results show that orangutans and a gibbon use information about the Where and What components in a foraging situation that attempted to simulate natural conditions. Thus, subjects' spatial memory included not only where items can be found but also what type of items. In contrast, we found only weak evidence that subjects also took into account the amount of food at each location. In general, subjects remembered food locations for each type of food from session to session as well as the fact they had visited a location within a session. We suggest that other important components come into play in the foraging situation such as the effect of social competition and the timing of the resource availability (i.e., When component).

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